ANNUAL CYCLE OF *LIMACINA RETROVERSA* IN PATAGONIAN WATERS

JOSÉ R. DADON
DEPARTAMENTO DE CIENCIAS BIOLOGICAS
FACULTAD DE CIENCIAS EXACTAS Y NATURALES
UNIVERSIDAD DE BUENOS AIRES
1428 BUENOS AIRES, ARGENTINA

ABSTRACT

An annual cycle (April 1978 - April 1979) of *Limacina retroversa* (Fleming) in Patagonian shelf and surrounding waters (40 - 55ºS) is analyzed. Both abundance and mesoscale distribution of this species in the area were strongly associated with the seasonal cycle. A stationary distribution pattern was evident in autumn and winter. The shelf population concentrated chiefly in a dense aggregation (maximum: 67,800 individuals per 1,000 m³) located to the northwest of the Malvinas Current. Individuals expatriated northward connected this aggregation with others carried by the core of the Malvinas Current. In October, the aggregation on the shelf began to disintegrate and proceeded slowly northward and off the shelf. The summer distribution pattern consisted of scattered individuals on the shelf and some aggregations moving along the slope.

Hydrological dynamics together with diel vertical migrations appeared to be of crucial importance in maintaining the observed distributions over shelf waters.

As with many other groups of marine zooplankters, pelagic mollusks have been little studied in the Southwestern Atlantic. Boltovskoy (1973, 1975) and Magaldi (1974, 1977) completed an inventory of the existing species and related the faunistic assemblages with megascale hydrological characteristics. However, their conclusions are based on a relatively small number of samples, which were not quantitatively, discontinuous in time, and obtained mainly from a reduced area between 35º and 40ºS.

In Patagonian waters south of 40ºS, only subantarctic species can be found (Dadon, 1984, 1986). Though poor in diversity, pelagic mollusks in these cold waters are abundant, reaching densities of 55,000 per 1,000 m³ on the slope and outer shelf during winter. *Limacina retroversa* (Fleming) was found to be the predominant species; the other planktonic mollusks were *L. helicina* (Phipps) and *Clio antarctica* Dall.

Seasonality in hydrographic conditions and biological production is very well known in Patagonian waters. Primary production peaks in September, October or November, depending on the latitude (Mandelli and Orlando, 1966; Carreto et al., 1981a). Zooplankton biomass increases in spring, following the period of high phytoplankton production (Ciechomski and Sanchez, 1983). This study is mainly concerned with seasonal patterns of *Limacina retroversa* in Patagonian waters. Monthly mesoscale distribution and changes in total abundance of the species during an annual cycle are analyzed and hypotheses are developed concerning the role of biological and environmental factors.

MATERIALS AND METHODS

Eighteen exploratory cruises were conducted in shelf and slope waters off Patagonia between April 1978 and April 1979 by the R/V "Walther Herwig" and " Shinkai Maru" (see Ciechomski et al., 1979; Cousseau et al., 1979). These collections included 539 samples taken to the south of 40ºS, all of which were analyzed for *Limacina retroversa*.

Samples were collected during daytime and twilight with Bongo nets (mouth diameter = 60 cm; length = 330 cm) fitted with 330 or 505 μm mesh nets. On the continental shelf, oblique tows extended from the surface to approximately 20 m above the bottom; on the slope, from the surface to 100 m depth. The maximal tow depth was estimated by time-depth recorders. The nets were provided with digital flow meters in both mouth openings and were towed at 3.5 knots. In all cases, the volume of water filtered through the nets was 200 - 1000 m³.

For counting, the samples were divided in aliquots with a Folsom plankton sample splitter until the final aliquot contained 180 to 300 individuals. Sparse samples were analyzed in their entirety.

For large volumes, little or no significant differences were obtained either in the plankton volume or in the size composition of the zooplankters, between the plankton volume filtered by the two meshes (Ciechomski and Sanchez, 1983).

HYDROLOGY

The Patagonian continental shelf is broad, with a gradual slope. Neritic waters are mostly of subantarctic origin with some admixture from continental run-off. Surface temperatures varied from 2.3 to 20.2ºC; in general, temperature increased northward and westward. Surface salinity varied from 34.17 o/oo (slope waters) to 32.39 o/oo (inner shelf waters). For detailed information about the physical data of the studied cruises see Ciechomski et al. (1979) and Cousseau et al. (1979).

The mesoscale hydrology of the area is dominated by the Malvinas or Falkland Current, which is a branch of the West Wind Drift (Fig. 1). Satellite observations (Legeckis and Gordon, 1982) show the Malvinas Current to be a well defined, 100 km-wide belt of cold waters. The core of this current runs close to the western boundary of the slope. Surface waters overlying the shelf also flow in the same general direction as the Malvinas Current, but at a considerably lower velocity. From the Gulf of San José (approximately 45º and 47ºS) to the slope, the Patagonian Coastal Current (Brandhorst and Castello, 1971) flows Northeast through the shelf (Fig. 1).

The contact between the Malvinas and Brazil currents constitutes the Subtropical-Subantarctic Front. This Front is located to the north of the Patagonian waters (Fig. 1) and constitutes a complex zone. It marks the limit of the distribution
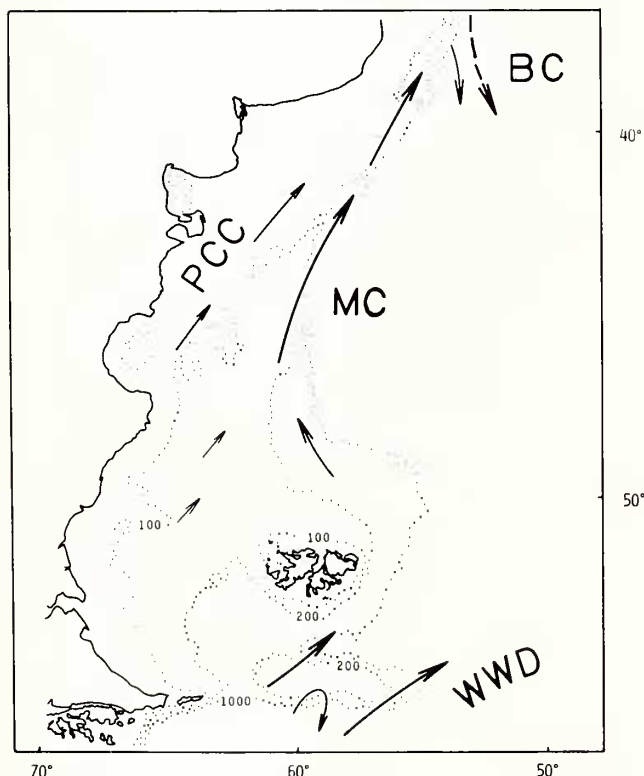

Fig. 2. Distribution of Limacina retroversa in May 1978. (Circles denote stations. Abundances as follows: Black areas indicate >1,000 per 1,000 m³; cross-hatched areas, 1,000 - 100 per 1,000 m³; hachured areas, 100 - 10 per 1,000 m³; white areas (when sampled) <10 per 1,000 m³).

of the subantarctic fauna in shelf waters and its position varies seasonally (Tseng, 1974; Olson et al., 1988).

RESULTS

SEASONAL DISTRIBUTION

The mesoscale horizontal distribution of Limacina retroversa in Patagonian waters showed a well defined pattern during the 1978 - 1979 annual cycle (Figs. 2-6). Densities higher than 1,000 individuals per 1,000 m³ (maximum of 67,800 per 1,000 m³) were found in slope waters throughout the year and in intermediate and outer shelf waters from April to September, 1978. In slope waters, dense aggregates were recorded that were transported northward by the Malvinas Current throughout the year (Figs. 2, 3, 6). In general, aggregates traveling in slope waters seemed to replace each other easily and quickly. Other authors (Bigelow, 1926; Redfield, 1939) pointed out the tendency of L. retroversa to aggregate.

The western limit for massive entrance of Limacina

Fig. 1. General hydrology of the study area (cold waters, full line; WWD, West Wind Drift; MC, Malvinas Current; PCC, Patagonian Coastal Current; Warm waters, hatched line; BC, Brazil Current).
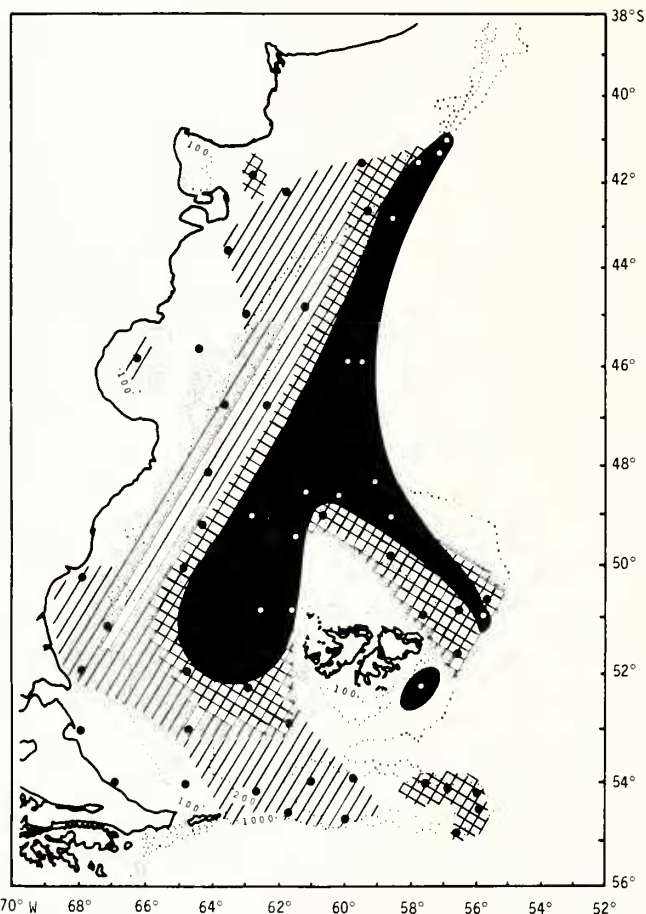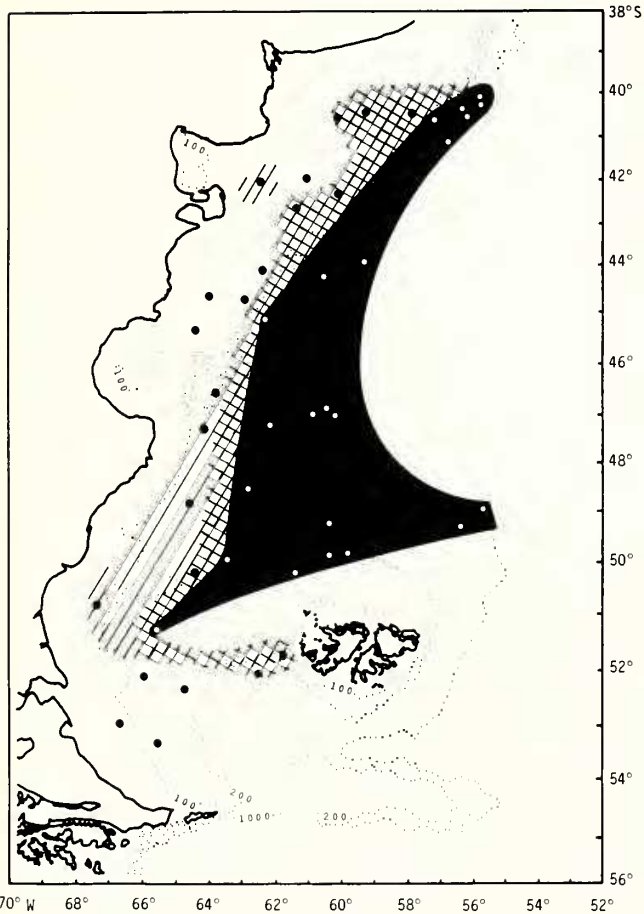
Fig. 3. Distribution of *Limacina retroversa* in June 1978. Symbols as in figure 2.

Fig. 4. Distribution of *Limacina retroversa* in October 1978. Symbols as in figure 2.

retroversa to the shelf coincided with the 100 m isobath to the south of 41ºS (Figs. 3, 5). Between this dense strip and the coast, low densities were only occasionally registered, especially to the north of 47ºS (Figs. 3, 4, 5). This low density or absence of the species constituted a tongue-like area which coincided with the path of the Patagonian Coastal Current. The holoplanktonic fauna depicted for this current is predominantly inner neritic [i.e. *Sagitta friderici* Ritter-Zahony, 1911 (Dadon and Mazzoni, 1989)]. Taking into account the geographical range of *L. retroversa* in the area, this species is oceanic but can tolerate neritic conditions.

In shelf waters, the highest densities were distributed in an oblong or pear-shaped configuration during the austral autumn and winter (Figs. 2, 3). The widest portion was located to the west of the Malvinas Islands and was continued as a band in a NNE direction onto the slope. This distribution was maintained without important changes practically from May until the beginning of spring. The only variations during this period were deformations and slight displacements of the aggregation towards the west (cf. Fig. 2 vs. Fig. 3). Same variations were observed for *Limacina helicina*, chaetognaths and cladocerans patterns (Dadon, 1986). Ramirez (1981) and Carreto *et al.* (1981b) pointed out that in winter, oceanic
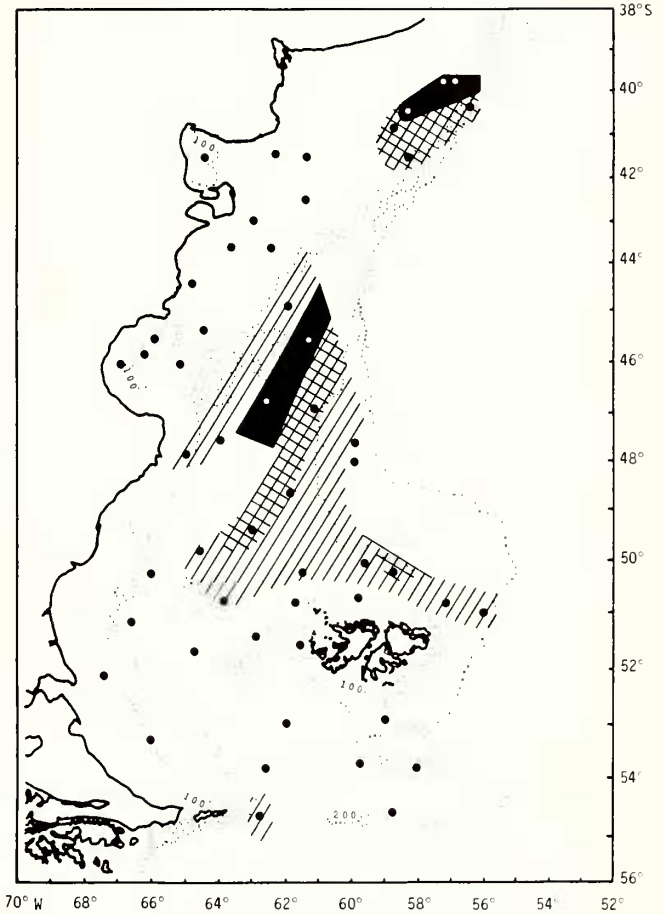
euphausiids, amphipods and copepods occurred predominantly on the Patagonian shelf, while typical neritic zooplankters were found in more offshore waters.

At the beginning of spring, a series of important changes in the distribution of *Limacina retroversa* on the continental shelf were observed (Fig. 4). The oblong aggregation began to disintegrate. Each fragment was carried to the northeast, reaching the slope at latitudes below 40ºS (Dadon, unpub. data). At least two of those isolated fragments were detected in October (Fig. 4), and two or three of them in November (Fig. 5). This process continued up to March 1979, when the last important concentration of organisms on the shelf was recorded between 43 and 45ºS (Fig. 6). The summer distribution pattern consisted of scattered individuals on the shelf and dense aggregations moving along the slope without penetrating the shelf, as shown between 39º and 42ºS in figure 6.

DENSITY IN RELATION TO ENVIRONMENTAL FACTORS

Limacina retroversa was found in waters when the surface temperatures ranged from 4.1 to 18.8ºC, and surface salinities were between 32.39 and 34.17 o/oo. The temperature

interval where the species was recorded in the Patagonian shelf waters (4 - 19ºC) was almost the same as the one recorded for the Southwestern Atlantic (see Spoel and Boltovskoy, 1981). Although densities higher than 1,000 per 1,000 m³ were found at 4.5 - 17.8ºC and 33.07 - 34.15 o/oo, this range was mainly recorded at 5 - 9ºC and >33.50 o/oo. These optima differ from those reported for northern hemisphere populations of *L. retroversa*: 8 - 10ºC and 34.5 - 35.0 o/oo in the North Atlantic (Chen and Bé, 1964); 7 - 12ºC in the Gulf of Maine (Bigelow, 1926); 7.5 - 10ºC in the Northeast Atlantic (Beckmann et al., 1987).

To obtain a simple relation between selected environmental factors and the species density in a given area, empirical relationships were sought. This analysis does not assume a direct cause-effect relationship, but, as Haedrich and Judkins (1979) pointed out, it constitutes a first necessary approximation to a very complex problem. Spatial variation in the density of *Limacina retroversa* density was compared to several environmental variables (depth, temperature, salinity and oxygen concentration) recorded during Cruises I and II of R/V "Shinkai Maru" (Cousseau et al., 1979). Association between density and each variable was determined by correlation analysis (Sokal and Rohlf, 1981). Data were normally distributed in all cases except for depth and density, for which the transformations $x' = x^{1/2}$ and $x' = \ln(x + 1)$ were applied, respectively.

The abundance of *Limacina retroversa* and the depth are positively correlated (Table 1), indicating that these organisms are denser in deeper waters. The correlation between density and temperature is negative, indicating that *L. retroversa* has a higher affinity for cold waters. However, the correlation between density and temperature decreases at greater depths. The strongest correlations between temperature and density were for the average temperature and for temperatures of the upper layers (surface to 20 - 25 m).

Confronted with the other environmental factors (Table 1), salinity shows lower correlation coefficients with density ($r < 0.39$; $P < 0.05$ or not significant). Dissolved oxygen concentration and density were positively correlated in all cases and, in contrast to temperature and salinity, the average did not show a higher value than its components when considered individually. The highest correlation values were achieved for oxygen concentration at depths between 0 and 45 - 50 m.

In order to establish the maximum proportion of the observed variation in the density of *Limacina retroversa* which can be explained in terms of the environmental variations, the
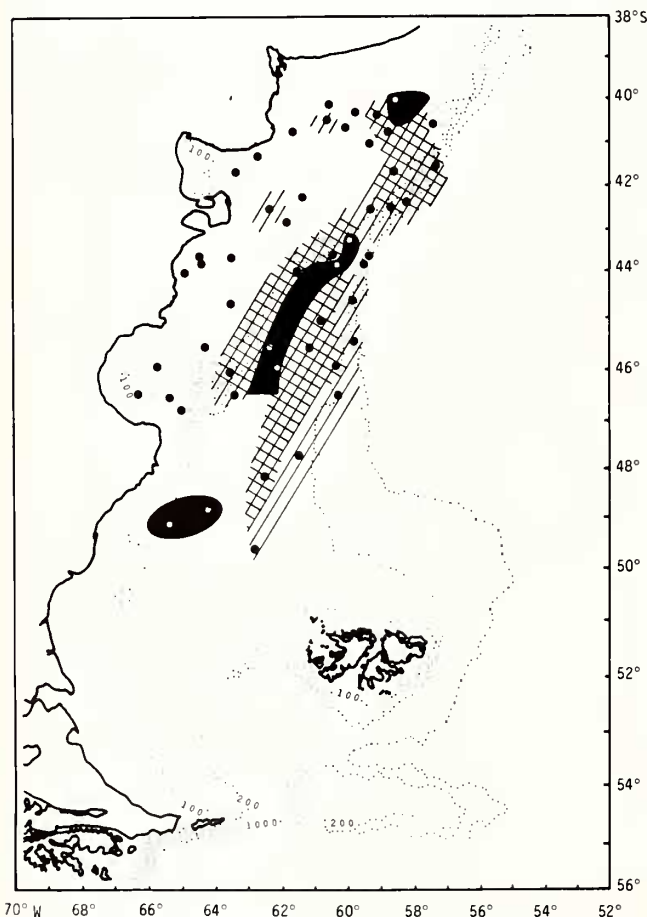

Fig. 5. Distribution of *Limacina retroversa* in November 1978. Symbols as in figure 2.
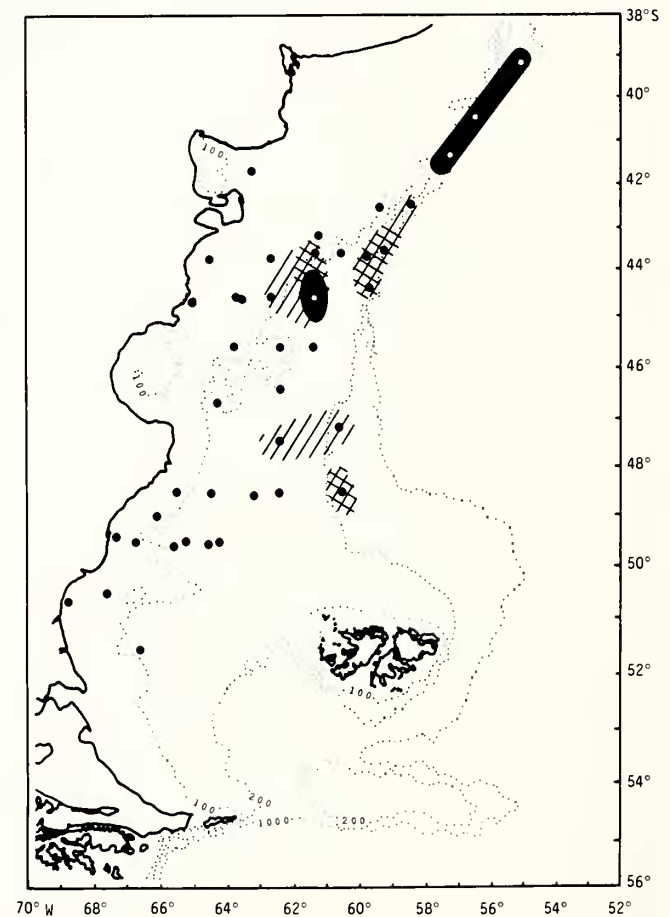

Fig. 6. Distribution of *Limacina retroversa* in March 1979. Symbols as in figure 2.

backward elimination and the forward selection procedures (see, for example, Drapper and Smith, 1966) were carried out considering the 25 environmental variables (Table 1) as predictors. The best regression equation was

$$Y = -90.748 + 4.308\ X_1 + 2.036\ X_2 \quad R^2 = 0.52$$

where Y: density of *L. retroversa*; X_1: oxygen concentration at 20 m; and X_2: average salinity. Since the most commonly-measured factors are temperature and salinity at the surface, their efficiency in predicting the species density either individually or in combination was analyzed for all months. Coefficients of determination ranked from 0.001 to 0.48 in all cases.

DISCUSSION

FACTORS GENERATING AND MAINTAINING MESOSCALE DISTRIBUTION

Detailed analysis of distribution and abundance patterns implies the study of the relations between the organisms and the environment. From Pickford (1946) on, several authors have repeatedly contended that the distribution of plankton is primarily ruled, or at least potentially governed, by the distribution of the water masses that the plankters inhabit. In certain cases, clear evidences in favor of this hypothesis were provided (see the review of Haedrich and Judkins, 1979; in pelagic mollusks, Furnestin, 1978). In other cases, this relation could be demonstrated only when intraspecific variations were considered (i.e. McGowan, 1963). In yet other cases, although the same species inhabited more than one water mass, there were remarkable differences in the density of individuals present in each environment, pointing out the necessity for quantitative studies when faunistic areas are to be compared (Fasham and Angel, 1975; Dadon, 1984). In many cases, however, this hypothesis had to be rejected because the species were ubiquitous or were highly cosmopolitan.

Limacina retroversa inhabits quite different water masses in the Southwestern Atlantic. It was collected on both sides of the Antarctic Convergence (Chen, 1968) and its geographical range extends northward to the Subtropical - Subantarctic Front. However, quantitative analyses (e.g. Bé and Gilmer, 1977: Fig. 7) have revealed that the area of highest densities is much less extensive and confined to the subantarctic region. Despite this clear association between *L. retroversa* and subantarctic waters, the present analysis of mesoscale distribution showed that the relationship is not simple and that it depends on several factors. As above mentioned, high densities of *L. retroversa* in patagonian waters were correlated with highly oxygenated, cold pelagic (= deep) waters. This set of correlations clearly defines the core of the Malvinas Current as the most favorable habitat in the area. This current is probably the only way for *L. retroversa* to enter the region, although the aggregates recorded in the core (i.e. in slope waters) seem to be rapidly expatriated northward. High densities associated with shelf waters, even when influenced by the Malvinas Current, established a stable distribution during autumn to winter. This stability implies the

Table 1. Correlation between density of *Limacina retroversa* and environmental variables (TD, tow depth; WA, weighted average for the sampled water column; r, correlation coefficient; **, P < 0.01; *, P < 0.05; NS, P > 0.05).

Environmental Variables		r	
Depth (m)		0.5376	**
Temp (ºC)	0 m	-0.6252	**
''	10 m	-0.6276	**
''	20-25 m	-0.6188	**
''	45-50 m	-0.5316	**
''	65-70 m	-0.3351	*
''	90-100 m	-0.3122	*
''	TD m	-0.6166	**
''	WA	-0.6546	**
Salinity (º/ₒₒ)	0 m	0.3166	*
''	10 m	0.3206	*
''	20-25 m	-0.2140	NS
''	45-50 m	0.3408	*
''	65-70 m	0.2701	NS
''	90-100 m	0.3101	NS
''	TD m	0.2448	NS
''	WA	0.3898	*
O₂ Conc (mg/l)	0m	0.6416	**
''	10 m	0.6320	**
''	20-25 m	0.6557	**
''	45-50 m	0.6372	**
''	65-70 m	0.5359	**
''	90-100 m	0.5605	**
''	TD m	0.5276	**
''	WA	0.5814	**

existence of steady environmental conditions, responsible for generating and maintaining (or at least, allowing) such a pattern.

Since plankton is transported passively, it is necessary to look for dynamic aspects of the oceanic environment. In an open area like the Patagonian shelf, a stable distribution necessarily implies a closed flow preventing massive, short-term expatriation of the organisms. *Limocina retroversa* inhabits the upper 150 m of the water column (Bé and Gilmer, 1977). Superficial hydrology of the area is predominantly unidirectional, i.e. through the area from south to north as an open flow. Conversely, deep layers are expected to flow at different velocities and directions.

While on the slope the Malvinas Current moves fast and unidirectional at all depths, on the shelf there are differences in the movements of the waters at different levels, as indicated by the theoretical winter current field calculated by Lusquiños and Schrott (1982). Between the surface and 20 m, current vectors on the continental shelf have a direction exclusively NNE, but at deeper levels (> 30 m), velocity decreases sharply and even reverses turning to the Southwest; this reversal is more important over the outer shelf south of 46ºS (Fig. 7). Comparing the winter distribution pattern of *L. retroversa* with this current field, the accumulation zone can be seen to lay within the area where the direction of the flow reverses. Diel vertical migrations of *L. retroversa* have been observed by several investigators (Bigelow, 1926; Chen and Bé, 1964). Thus, individuals migrate through layers
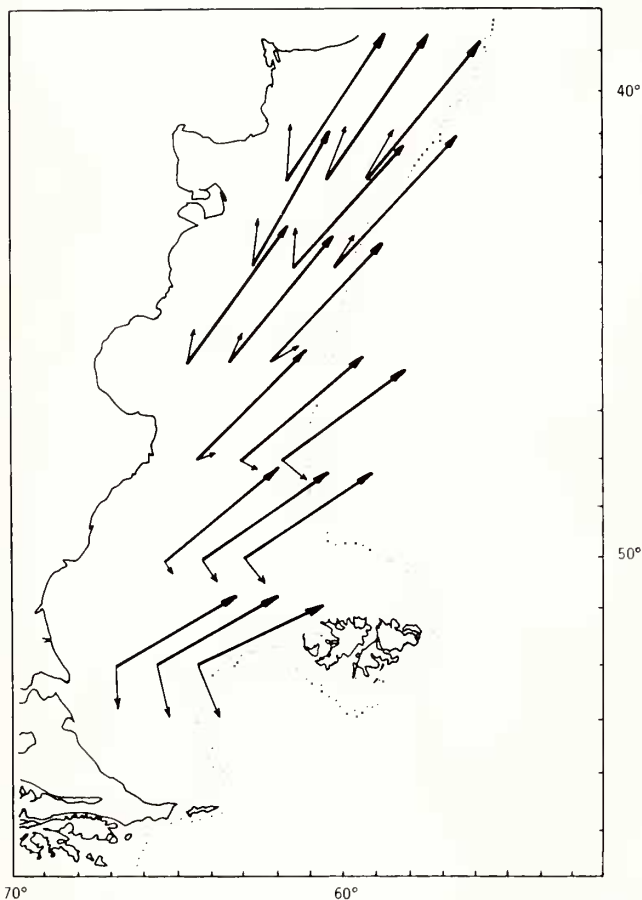
Fig. 7. Theoretical winter field of currents (according to Lusquiños and Schrott, 1982) (thick arrows, 0 m; thin arrows, 50 m).

which move at different velocities and even in opposite directions. The bulk of the individuals in the area prevent massive expatriation, retrogressing during the day the way they progressed during the night. On the other hand, irreversibly expatriated individuals would gradually approach the continental slope, as a band connecting the aggregation area and the slope (Figs. 2, 3). This mechanism would explain the shape and the long-term stability of the aggregate on the continental shelf.

SEASONAL CHANGES

Typically, a marked seasonality is shown in Patagonian waters, both for environmental and biological factors. During autumn and winter, the cooling of waters is uniform and smooth; on the contrary, warming of the water column during the warm period is sharp (Krepper and Bianchi, 1982). Temperature gradients between the coast and the slope became more distinct during spring and summer than the ones observed during fall and winter (Branshorst and Castello, 1971; Legeckis and Gordon, 1982). The primary production peaks during September in the northern area and this pulse displaces to the south reaching the southern extreme in November (Carreto et al., 1981a). The highest chlorophyll con-

centrations (100 - 200 mg/m²) were detected between 44⁰ and 47⁰S (Carreto et al., 1981a). Zooplankton production follows a similar pattern, though slightly delayed (Ciechomski and Sanchez, 1983). During the 1978 - 1979 cycle, the highest zooplankton densities were registered by Ciechomski and Sanchez in November in the northern portion (42 - 44⁰S) and in summer in the south (51 - 53⁰S). Evidences of massive spawning in shelf waters during November 1978 were also found for oceanic zooplankters which, like *L. retroversa*, are transported to the outer shelf by the Malvinas Current (e.g. euphausiids; see Ramírez and Dato, 1983). According to this, a springtime pulse of *L. retroversa* should be expected coinciding with this increase in general zooplankton production.

After November, the abundance of *L. retroversa* diminished as well as the area occupied by the species on the continental shelf. The last remnants of the dense core which had occupied the major part of the continental shelf were detected towards the end of summer, in March 1979, between 43 and 45⁰S (Fig. 6). Over the rest of the shelf, and especially in the southern portion, *L. retroversa* was present only occasionally and always in very low densities (< 10 per 1,000 m³). Nonetheless, even when abundance over the shelf was lower in April 1979, densities up to 100 per 1,000 m³ were detected in neritic waters south of 47⁰S, indicating the beginning of a new cycle. According with these observations, not only the reproduction but also the massive inmigration seem to show a seasonal pattern.

Seasonal patterns in abundance and/or horizontal distribution have been previously described for *Limacina retroversa* in other regions (Redfield, 1939; Vane and Colebrook, 1962; Paranjape and Conover, 1973). The annual cycle of this species on Patagonian shelf waters shows some similarities with that described by Redfield (1939) for the Gulf of Maine. In both areas, *L. retroversa* is alternately repatriated and expatriated in large numbers and cannot be maintained from one year to the next by means of *in situ* reproduction alone. The dynamics for this species and, probably, for most oceanic species of zooplankton, is predominantly regulated by migratory events. This is clearly evident in the core of the Malvinas Current (on the continental slope), where aggregations are rapidly transported northward, but also in shelf waters. In the latter, even when seasonal changes in the local hydrology allow a temporary residence, and eventually reproduction, they cannot preclude a final expatriation. In this context, the Patagonian waters can be described as a subsidiary system, a one-way transit via connecting the West Wind Drift with the Transition Zone in which the long-term presence of the oceanic zooplankton depends on the production surplus coming from other systems.

ACKNOWLEDGMENTS

LITERATURE CITED

Bé, A. W. H. and R. W. Gilmer. 1977. A zoogeographic and taxonomic review of Euthecosomatous Pteropoda. *In: Oceanic Micropaleontology, Vol. 1*, A. T. S. Ramsay, ed. pp. 733-808. Academic Press, London.

Beckmann, W., A. Auras and Ch. Hemleben. 1987. Cyclonic cold-core eddy in the eastern North Atlantic. III. Zooplankton. *Marine Ecology Progress Series* 39:165-173.

Bigelow, H. B. 1926. Plankton of the offshore waters of the Gulf of Maine. *Bulletin of the United States Bureau of Fisheries* 40(2):1-509.

Boltovskoy, D. 1973. Los Euthecosomados del Mar Argentino y adyacencias (Mollusca, Pteropoda). *Physis (Buenos Aires)* A, 32(85):395-411.

Boltovskoy, D. 1975. Ecological aspects of zooplankton (Foraminifera, Pteropoda and Chaetognatha) of the Southwestern Atlantic Ocean. *Veliger* 18(2):203-216.

Brandhorst, W. and J. P. Castello. 1971. Evaluación de los recursos de anchoíta (*Engraulis anchita*) frente a la Argentina y Uruguay. I. Las condiciones oceanográficas, sinopsis del conocimiento actual sobre la anchoíta y el plan para su evaluación. *Contribuciones del Instituto de Biología Marina (Mar del Plata, Argentina)* 166:-1-63.

Carreto, J. I., R. Negri and H. Benavides. 1981a. Fitoplancton, pigmentos y nutrientes. Resultados de las campañas III y VI del B/I "Shinkai Maru", 1978. *In: Campañas de investigación pesquera realizadas en el Mar Argentino por los B/I "Shinkai Maru" y "Walther Herwig" y el B/P "Marburg", años 1978 y 1979. Resultados de la Parte Argentina*, V. Angelescu, ed. pp. 181-201. Contribuciones del Instituto Nacional de Investigación y Desarrollo Pesquero 383, Mar del Plata, Argentina.

Carreto, J. I., F. C. Ramírez and C. Dato. 1981b. Zooplancton y producción secundaria. Parte II. Distribución y variación estacional de la biomasa zooplanctónica. *In: Campañas de investigación pesquera realizadas en el Mar Argentino por los B/I "Shinkai Maru" y "Walther Herwig" y el B/P "Marburg", años 1978 y 1979. Resultados de la Parte Argentina*, V. Angelescu, ed. pp. 213-232. Contribuciones del Instituto Nacional de Investigación y Desarrollo Pesquero 383, Mar del Plata, Argentina.

Chen, Ch. 1968. Zoogeography of thecosomatous pteropods in the West Antarctic Ocean. *Nautilus* 81(3):94-101.

Chen, Ch. and A. W. H. Bé. 1964. Seasonal distribution of Euthecosomatous pteropods in the surface waters of five stations in the Western North Atlantic. *Bulletin of Marine Science of the Gulf and Caribbean* 14(2):185-220.

Ciechomski, J. D. de, M. D. Ehrlich, C. A. Lasta and R. P. Sánchez. 1979. Exploratory cruises carried out by the Fisheries Research Vessel "Walther Herwig", in the Argentine Sea, from May to November 1978. Organization and record of basic data obtained. *Contribuciones del Instituto Nacional de Investigación y Desarrollo Pesquero (Mar del Plata, Argentina)* 374:1-312. (In Spanish and English).

Ciechomski, J. D. de and R. P. Sanchez. 1983. Relationship between ichthyoplankton abundance and associated zooplankton biomass in the shelf waters off Argentina. *Biological Oceanography* 3(1):77-101.

Cousseau, M. B., J. E. Hansen and D. L. Gru. 1979. The exploratory cruises carried out by the Japanese vessel "Shinkai Maru" in the Argentine Sea, from April 1978 to April 1979. Organization and record of basic data. *Contribuciones del Instituto Nacional de Investigación y Desarrollo Pesquero (Mar del Plata, Argentina)* 373:1-625. (In Spanish and English).

Dadon, J. R. 1984. Distribución y abundancia de Pteropoda Thecosomata en el Atlántico Sudoccidental. *Physis (Buenos Aires)*, A, 42(102):25-38.

Dadon, J. R. 1986. Distribución y abundancia de Pteropoda Thecosomata (Mollusca, Gastropoda) del Mar Epicontinental Argentino y adyacencias. Junio y julio de 1978. *Physis (Buenos Aires)*, A, 44(106):43-50.

Dadon, J. R. and H. E. Mazzoni. 1989. Aspectos biogeográficos de Thecosomata (Gastropoda) y Chaetognatha del Mar Argentino. *In: Resúmenes de la XIV Reunión Argentina de Ecología, Universidad Nacional de Jujuy (Argentina)*. p. 161.

Drapper, N. and H. Smith. 1966. *Applied regression analysis*. John Wiley & Sons, Inc. New York, London, Sydney. 407 pp.

Fasham, M. J. R. and M. V. Angel. 1975. The relationship of the zoogeographic distributions of the planktonic ostracods in the North-east Atlantic to the water masses. *Journal of Marine Biology Association of the United Kingdom* 55:739-757.

Furnestin, M. L. 1978. Planktonic molluscs as hydrological and ecological indicators. *In: Pathways in Malacology*, S. van der Spoel, ed. pp. 175-194. Bohn, Scheltema & Holkema, Utrecht.

Haedrich, R. L. and D. C. Judkins. 1979. Macrozooplankton and its environment. *In: Zoogeography and diversity of plankton*, S. Van der Spoel and A. C. Pierrot-Bults, eds. pp. 4-28. Bunge Scientific Publishers, Utrecht.

Krepper, C. M. and A. Bianchi. 1982. Balance calórico del Mar Epicontinental Argentino. *Acta Oceanographica Argentina* 3(1):119-133.

Legeckis, R. and A. L. Gordon. 1982. Satellite observations of the Brazil and Falkland Currents.- 1975 to 1976 and 1978. *Deep-Sea Research* 29(3A):375-401.

Lusquiños, A. J. and A. G. Schrott. 1982. *Corrientes en el Mar Epicontinental Argentino en invierno*. Subsecretaría de Ciencia y Tecnología, Argentina. 81 pp.

Magaldi, N. 1974. Moluscos holoplanctónicos del Atlántico Sudoccidental. I. Pterópodos euthecosomados colectados por el "Atlantis" en Marzo 1971. *Comunicaciones de la Sociedad Malacológica del Uruguay* 4(27):1-34.

Magaldi, N. 1977. Moluscos holoplanctónicos del Atlántico Sudoccidental. III. Heterópodos y pterópodos de aguas superficiales brasileñas y uruguayas. *Comunicaciones de la Sociedad Malacológica del Uruguay* 4(33):295-320.

Mandelli, E. F. and A. M. Orlando. 1966. La producción orgánica primaria y las características de la Corriente de Malvinas. *Boletín del Servicio de Hidrografía Naval, Buenos Aires* 3(3):185-195.

McGowan, J. A. 1963. Geographical variation in *Limacina helicina* in the North Pacific. *Speciation in the Sea. Systematics Association Publication* No. 5:109-128.

Olson, D. B., G. P. Podestá, R. H. Evans and O. B. Brown. 1988. Temporal variations in the separation of Brazil and Malvinas Currents. *Deep-Sea Research* 35(12A):1971-1990.

Paranjape, M. A. and R. J. Conover. 1973. Zooplankton of St. Margaret's Bay. 1968 to 1971. *Technical Reports of the Fishery Board of Canada* 401. 83 pp.

Pickford, G. E. 1946. *Vampyroteuthis infernalis* Chun. An archaic dibranchiate cephalopod. I. Natural history and distribution. *Dana Reports* 29:1-40.

Ramírez, F. C. 1981. Zooplancton y producción secundaria. Parte I. Distribución y variación estacional de los copépodos. *In: Campañas de investigación pesquera realizadas en el Mar Argentino por los B/I "Shinkai Maru" y "Walther Herwig" y el B/P "Marburg", años 1978 y 1979. Resultados de la Parte Argentina*, V. Angelescu, ed. pp. 202-212. Contribuciones del Instituto Nacional de Investigación y Desarrollo Pesquero 383, Mar del Plata, Argentina.

Ramírez, F. C. and C. Dato. 1983. Seasonal changes in population structure and gonadal development of three Euphausiid species. *Oceanologica Acta* 6(4):427-433.

Redfield, A. C. 1939. The history of a population of *Limacina retroversa* during its drift across the Gulf of Maine. *Biological Bulletin* 79:459-487.

Sokal, R. R. and F. J. Rohlf. 1981. *Biometry*. W. H. Freeman and Co., New York. 859 pp.

Spoel, S. Van der, and D. Boltovskoy. 1981. Pteropoda. *In: Atlas del zooplancton del Atlántico Sudoccidental y métodos de trabajo con el zooplancton marino*, D. Boltovskoy, ed. pp. 493-524. Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, Argentina.

Tseng, Y. C. 1974. Study of the surface boundary of the Brazil and Falkland Currents. *In: Seminar on space applications of direct interest to developing countries*. 2:160-173. Instituto de Pesquisas Espaciais, Saõ José dos Campos, Saõ Paulo, Brasil.

Vane, F. R. and J. M. Colebrook. 1962. Continuous plankton records: Contribution towards a plankton atlas of the North-Eastern Atlantic and the North Sea. Part VI: The seasonal and annual distribution of the Gastropoda. *Bulletin of Marine Ecology* 5(50):247-253.